THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

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(*Concluded from p. 367.*)

B. MESOPHYTIC DIVISION (MESOPHYTIA) CULTURE SECTION.

Consists of plants requiring the normal climatic and soil conditions of this region, useful to man and kept by his care in certain definite artificial groups.

II. RECLAIMED SALT MARSH FORMATION (MEADOW FORMATION, POIUM).

Consists, in adaptation to the very fine and hence poorly-aerated but evenly-moistened soil, of slender-rooted surface-following and hence herbaceous plants, in this case grasses or grass-like plants useful for forage or grain. Owing to the peculiar conditions here prevailing in the form of a newly-opened field (see page 295), no care from man directly is necessary to keep the plants in their desirable economic condition, for both seeding and resistance to undesirable immigrants take place naturally as long as he preserves the field in its best condition.

Includes, within an enclosure of dikes, the greater part of the area of the original salt marshes, from the sea to the head of tide on the rivers, and extended artificially into the lakes of the bogs and the bogs themselves (page 179). The formation includes three associations.

4. THE PHLEUM-AGROPYRUM, OR TIMOTHY-COUCH ASSOCIATION, OR PHLEUMETUM.

The characteristic, prevailing and most valued association of the perfectly reclaimed marsh, occurring everywhere on the higher parts of the marsh within the dikes where the drainage is good, and where the marsh soil has not been exhausted or has

not roads nor bald spots (*figs. 7, 8*). Distinguished by its familiar hay-meadow aspect, though with an unusual prevalence of couch and unusual density, luxuriance and purity of the grasses.

The association is composed of two dominant members of nearly equal prominence, with several secondary and many subordinate members, and frequent visitors.

PHLEUM PRATENSE L. Timothy.—The most abundant, characteristic, and valuable plant of the reclaimed marsh, and the dominant member of the Phleumetum. It is confined to well-drained and salt-free places, but takes possession wherever these conditions are found, hence on the highest and oldest marsh, along ditch ridges and to some extent on dikes, particularly those not exposed to the dash of the sea, and reaching its greatest perfection on the banks of aboideaued creeks. In the reclamation of marsh it is the last of the natural sequence of forms and apparently can maintain itself indefinitely as long as the drainage is kept up. It is killed immediately by salt water.

A familiar vegetation-form, typical of the grasses. Its root-hairs are plasmolyzed by 30 per cent. or less of salt water. Not native; introduced from Europe.

AGROPYRUM REPENS Beauv. Couch.—Second to the preceding in abundance and luxuriance on the reclaimed marsh, and in places even exceeding and replacing it. It forms here a highly valued hay, little inferior to timothy. It extends also upon the dikes and is the characteristic dike-top grass, especially on the dikes exposed to occasional wash from the sea, including the old abandoned dikes on the salt marsh. It also tends to come in upon the highest parts of the Staticetum.

Vegetation-form very like timothy, but able to stand salter, though not wetter places than the latter. Its root-hairs endure 30 per cent. pure salt water without plasmolysis. A native plant, found also in Europe; doubtless the form on these marshes is introduced with the timothy from Europe.

AGROSTIS ALBA L. Brown top. (Includes also *A. vulgaris*, not now considered distinct.)—Distinctly third in importance of the forms of the reclaimed marsh, occurring intermixed with the two dominant forms, but tending to occupy especially the margins

of the drainage furrows, and the lower ground, where, especially on poor marsh, it often replaces entirely the other two and becomes the dominant form. Along the roads and in places somewhat salt, it is much dwarfed. It is one of the first forms to come upon the reclaimed marsh, following after the members of the Salicornetum and Staticetum.

Vegetation-form and adaptations not especially studied; evidently more halophilous and hydrophilous than the preceding.

TRIFOLIUM PRATENSE L. Red clover.—Occurs as a characteristic companion with timothy, under whose shade it thrives everywhere on the best marsh. It varies greatly in quantity in different years, sometimes being extremely abundant (locally "clover-years"), and sometimes being nearly wanting, perhaps because it is killed by some winters and requires two years to reach full maturity.

Vegetation-form and adaptations not specially studied, but its power of fixing nitrogen comes here into account, and possibly some relation of a remotely symbiotic sort exists between it and the timothy. It is immediately killed by salt water.

TRIFOLIUM HYBRIDUM L., alsike, and T. REPENS L., white clover, also occur, but less abundantly. The two former are introduced from Europe, but the latter is native.

CHRYSANTHEMUM LEUCANTHEMUM L. Bulls-eye daisy.—Abundant in places and somewhat gregarious, and in other places wanting. Apparently it cannot compete with the timothy and couch on the best places but comes in where conditions are less perfect for those two forms. Not native, but from Europe.

Other secondary forms of minor importaace are:

Alopecurus pratensis L., bastard timothy or Durgin timothy. Rather abundant in places, and an injury to the hay-fields through its early ripening.

Calamagrostis Canadensis Beauv., blue-joint, occurs in occasional patches, but belongs rather with the hydrophytic associations.

Poa pratensis L. Occasional.

Lolium temulentum L.

Danthonia spicata Beauv.

Agrostis scabra Willd. [*A. hyemalis* (Walt.) B. S. P.]

Lathyrus palustris L. Rather common in spots on good marsh.

Ranunculus acris L. Buttercup. In patches on poorer marsh, not abundant.

Other plants occurring amongst the grasses as subordinate members or visitors are: *Fragaria virginica* L., strawberry; *Achillea millefolium* L., yarrow; *Leontodon autumnale* L., fall dandelion; *Brunella vulgaris* L.; *Viola* spp.; *Cerastium* spp.; *Epilobium lineare* Muhl., *Rumex Britannica* L.; *Rhinanthus Cristagalli* L.; *Euphrasia officinalis* L.; *Aster Novi-Belgii* L.; *Lactuca leucophaea* Gray; *Solidago neglecta* T. & G. Along the ditches grows *Convolvulus sepium* L., and there are many others.

The general adaptations of these forms to this habitat are sufficiently plain; they are typical mesophytic grasses, and the reclaimed marshes offer, as has already been traced, a typical habitat for them. But when we pass to details, the subject is not so clear.

The two dominant members, the timothy and couch, occur variously intermingled, at times in about equal proportions and again with one or the other more abundant, even to such a degree that one may occur without the other for long stretches. No physical cause is traceable for these differences, beyond the fact that the timothy seems to have the advantage on the very best parts of the marsh, and the couch where salt is more abundant. Wherever they occur intermingled, patches of one or the other often exist without visible physical determinants; and their appearance gives the impression of a resultant of slight disturbances of equilibrium in the struggle between two evenly-matched forms (or else an adjustment between two mutually tolerant forms), here one and there the other, through the slightest causes, obtaining the advantage. Both plants seem to attain their greatest perfection and purity upon the banks of the aboideaued creeks, where no doubt the somewhat coarser soil, together with the better drainage, affords a better aeration for the roots, thus permitting the more luxuriant growth. At these and other places a marked phenomenon is to be observed, having no doubt an important bearing upon the nature of competition, namely, wherever these forms are most luxuriant, there the secondary and occasional forms are less abundant, and the latter come in with the decreasing vegetative vigor of the dominant forms. In the wetter, salter, and poorer marsh the Agrostis appears more abundantly, thus forming the marginal member in that direction, as couch does in the other; but in addition it forms in places on

low marsh great areas, to the exclusion of the dominant members, in such places becoming itself the dominant form. One cannot, however, trace all of the transitions to physical causes, and in places it seems as if we were dealing here with another case of unstable equilibrium, the forms acting in mass against one another. The same phenomenon appears in the bulls-eye daisy, groups of which appear amongst the dominant members in an apparently very irregular way, again suggesting that it is not physical causes alone which are responsible for their distribution, but that it is either the result of a struggle between nearly equally-matched masses of forms, or else that there is a large measure of pure accident in the details of their distribution relatively to one another. But of this we can know nothing until we learn how the forms "compete" with one another.

This association shows one very characteristic feature of an association, lacking in those heretofore considered, namely, a distribution of the aerial parts of its members in horizontal strata. Forming the uppermost layer in the full blaze of the sun come the two dominant grasses. Nestling below the shade of their leaves, come the clovers and the Lathyrus, while in a third layer nearer the ground are the leaves of the violets, strawberries, and other low forms which I have not tried to list, all of which, of course, blossom in the early spring before the grasses have grown tall. Here again we are faced by the question as to the real ecological interrelationships of these various forms, whether we have to do (1) purely with a mixture of forms, some of which happen to be able to live in the interstices left in the growth of other forms, or (2) whether the smaller derive some benefit from the shade or other protection of the taller, or (3) whether there may be some advantage to all the members from the association, such as we can imagine the taller timothy derives from the smaller but nitrogen-fixing clover. On these matters we still have no knowledge.

As above stated, the marginal member of the association towards the Staticetum is the couch, and the marginal member towards the Macrospartinetum is the brown top, while that towards the Cnicetum is the bulls-eye daisy.

Considering now the relation of this to the other associations, it is very important to note that it is the natural association for its situation, and has not to be brought into its typical condition nor kept there by the cultivation so necessary on the upland hay meadows. When a piece of marsh is diked and drained, there follows, as we shall later note, a perfectly natural succession of plants, from the Staticetum to the Phleumetum, without any care or seeding, and the Phleumetum therefore represents the best adapted type of vegetation in this region to the conditions of the reclaimed marsh. And it is important to notice that the timothy, and no doubt also the couch, are not native, but introduced forms. There were in this forested region no mesophytic native plants so well adapted to this new field as the open-ground hay grasses from Europe, a point in perfect harmony with the general principles controlling the relations of introduced to native plants as set forth by Gray in his essay "On the pertinacity and predominance of weeds." As long as the drains are kept up, and until by long years of cropping the soil begins to weaken, this association holds its own against all comers of every sort. There is no tendency here for forest to come in, as on the upland, for reasons already explained (p. 291), nor can the ordinary weeds gain a footing until the timothy weakens through exhaustion of the soil or other cause, in which case, some scanty approach to forest may occur (p. 293). On these marshes, therefore, these European hay-grasses find an even more congenial and competition-free field than upon the upland meadows. When, however, the drainage becomes imperfect, the brown top rises to prominence, and that in turn gives way to the broadleaf as the water becomes more abundant. In these phenomena of replacement we see illustrated the first principle of competition, that a form can hold its own only in the vicinity of its optimum, and beyond that it goes down readily before another form whose optimum is being approached.

5. THE ROADSIDE WEED ASSOCIATION, OR CNICETUM.

In addition to the "weeds" associated naturally with the Phleumetum, there occurs a distinct association of upland weeds in certain places on the marshes. As this association is by no

means characteristic of the marsh, being but an extension of that of the upland, where its consideration belongs, and moreover as it is of very subordinate importance in the marsh vegetation it need here be considered but very briefly.

On the marshes the association occurs only in places especially freed from salt. Thus it occurs especially along the inner slopes of the dikes, above the frequent zone of Atriplex, and below the capping of couch (*fig. 15*), that position being particularly well freed of its salt by the excellent drainage and protection from the occasional salt spray dashed against the outer face of the dikes. In such places occur Scotch and Canada thistles (*Cnicus*, giving name to the association), yarrow in great abundance, docks, strawberry, chickweeds and many others of characteristic appearance. Again, on the ridges of earth made by the mud thrown up from the ditches, the association again appears, but here, for reasons already explained (p. 293), it tends to include some shrubs, spiraeas, wild roses, rarely alders, and a few others, with occasionally small birches, almost the only situation indeed, in which any trees are able to exist upon the marsh. There is another situation in which the association is particularly well developed, namely, on the railway embankment built, but never used, across the marshes of the Shepody near the head of tide. On this embankment, built entirely of the marsh mud, the weeds have possession, and form a tangle of spiraeas, thalictrum, yarrow, bindweed, goldenrods, myrica, sorrels, lysimachia, evening primroses, and even some lichens, small white birch and others, a genuine upland association despite the marsh soil. Another situation in which the association is well developed is on the sites of the occasional hay ricks and the vicinity of the barns on the marshes. In the former situation the bindweed is especially characteristic, and in the latter the chickweeds, but in both cases many others are associated with them. At first sight these situations, directly upon the surface of the marsh, would appear too salt to maintain such a vegetation, but, as already explained (p 293), the conditions there are really such as to promote the removal of salt. Here and there among the Phleumetum some

of these weeds may appear, but never in any abundance. Finally there are those places on the flat shallow marsh already mentioned (p. 293), from which the salt appears to have been largely removed, where a growth of bushes with some weeds may appear. These spots are of some interest as showing the tendency of the marsh, when freed from the hindering influence of the salt, to develop the climatic type of vegetation for this region, namely, the forest.

C. HYDROPHYTIC DIVISION.

Consists of plants of various aspect, but typically of soft texture and small to moderate size, provided with abundant air system enabling them to thrive in part or in whole in standing water. Contains here four formations.

III. THE WET-MARSH FORMATION.

Consists of plants capable of enduring much but not constant standing water at the roots, but otherwise able to meet the conditions of the meadow; hence composed mostly of grasses and similar forms.

Occupies all places with constant capillary but only occasional hydrostatic fresh water, hence occuring in bands between the high marsh, whether reclaimed or salt, and the bogs, and coming in on reclaimed marsh wherever the drainage is neglected. It occupies very extensive areas, perhaps equaling the Phleumetum in extent and readily distinguished from the latter by the brighter green color of at least a part of it.

It is composed of two associations.

6. THE SPARTINA CYNOSUROIDES, OR BROADLEAF ASSOCIATION, OR MACROSPARTINETUM.

The characteristic association of the reclaimed marshes wherever drainage is poor but standing water is usually absent, and hence occupying great areas on the lower parts of the marshes away from the rivers and sea and between the Phleumetum and the bog (*figs. 7, 8*). The bad aeration of the soil permits the change to blue clay earlier discussed (p. 288), which seems usually to underlie the association. The association is readily distinguished to the eye by the large size, grace-

ful habit and bright green color of its dominant form, the broadleaf.

The association is composed of but a single truly dominant member but with several secondary forms.

SPARTINA CYNOSUROIDES Willd. Broadleaf.—Preeminently the character-plant of the reclaimed wet marsh, great areas of which consist of it almost exclusively. It occurs also around the margins of the freshwater lakes and streams, to a slight extent upon the matured Staticetum, along the tide-water and nearly fresh ditches, on the new mud of the lakes in reclamation and in the bottoms of aboideaued streams. It is of very great economic importance as hay, second only in value to the timothy and couch.

Its vegetation-form embraces the usual grass type, but with unusually large air-passages, luxuriant and markedly mesophytic structure, and a considerable power of salt resistance in its roots. Will stand considerable tiding. Its root-hairs endure nearly 50 per cent. of salt water without plasmolysis, and very likely have a specific power of resistance to the somewhat poisonous constituents of the blue-clay.

CICUTA MACULATA L. Called locally (by one person) caraway (sic).—Very abundant in places among the broadleaf, raising its upper leaves and flowers much above that form and so abundant that when in flower it gives the marsh a whitish look from a distance. It is a poisonous plant, but leaves and stems appear not to be injurious when dry, though horses have been supposed to have been poisoned by eating the roots.

CAREX MARITIMA O. F. Mueller. Watergrass or fresh-water grass.—The characteristic form where there is standing water in isolated places on the marsh, in such places often replacing the broadleaf, though usually more or less intermingled with it. It stands salt water well in tiding.

CALAMAGROSTIS CANADENSIS Beauv. Blue joint.—Occurs in places as a secondary member in the wet marsh, often in large closed patches, but especially along the ditches and toward the bogs, and along the courses of the streams in the bogs, where it sometimes grows in long, dense, closed masses. Also in places upon the dry marsh in the Phleumetum.

SCIRPUS ATROVIRENS Muhl. Kill-cow (sometimes three-square?). In the wettest places, and sometimes abundant, replacing the watergrass.

Of minor importance in this association is *Triglochin maritima* L., which occurs scattered amongst the broadleaf and watergrass, and appears as much at home as upon the Staticetum. Also there occur, in a subordinate rôle, *Thalictrum polygamum* Muhl., in occasional patches; *Epilobium lineare* Muhl., abundant in places; *Lysimachia stricta* L. [*L. terrestris* (L.) B. S. P.], abundant; *Iris versicolor* L.; *Campanula aparinoides* Pursh; *Scutellaria galericulata* L., and many others of lesser importance.

The power of the chief members to endure their wet situations is sufficiently explained by their capacity for air-storage, and their ability to stand some salt by their power of root resistance. Of these members at least three, *Carex maritima*, the broadleaf, and the Triglochin, are more or less halophilous, and it is at first surprising to find them thriving so well in this situation. It is very likely, however, that this position is more salt than it seems, for it must receive much of the drainage from the higher marsh (to which, as we have seen, much salt is being raised from below by evaporation), and this may be the case particularly in the low places where *Carex maritima* abounds. This can only be determined by analysis of the soil water in that situation. It may be possible, too, that a capacity to endure salt does not carry with it any lessened capacity to endure its absence, an important point still to be determined.

The broadleaf is the overwhelmingly dominant member of this association, no other approaching it in importance, and it often occurs for great areas practically pure. The Cicuta, raising most of its foliage above that of the broadleaf, is far the most prominent secondary member, but its exact relations with the broadleaf, whether of competition, mutual tolerance or mutual advantage, remain to be determined. The marginal member toward the Phleumetum is the broadleaf itself, as it is toward Staticetum. In the former case it meets the Agrostis, and in the latter appears upon the matured salt marsh, and no doubt in the original unreclaimed condition of the marshes it occupied the great areas between the Staticetum and the bogs. The marginal member toward the bog is sometimes the broadleaf and some-

times the watergrass. The association as a whole goes down very readily before the bog-marsh, which is constantly tending to invade it, and which has to be constantly fought by the marsh-farmers, partly by improving the drainage and partly by the admission of the tide.

7. THE CAREX-ASPIDIUM, OR BOG-MARSH ASSOCIATION, OR ASPIDETUM.

The characteristic association of the transition from Macrospartinetum or broadleaf, to bog,[43] occupying the places with constant hydrostatic water in the soil, but with little above it, resulting in a mixture of grass-like and bog-like plants. Where the transition from broadleaf to bog is gradual this band is wide, elsewhere narrow or wanting. It is marked by four dominant forms.

SPHAGNUM RECURVUM vars. PARVIFLORUM (Sendt.) Warn., and IMBRICATUM (Hornsch.),[44] with very likely others.—The most characteristic plant of this association, and the invariable leader of its advance upon the broadleaf.

CAREX FILIFORMIS L.—A very characteristic member of the association, often abundant enough to give it the appearance of a meadow. Vegetation-form not studied.

ASPIDIUM THELYPTERIS Swartz. *Dryopteris Thelypteris* (L.) A. Gray.—Very abundant and a characteristic member of the association. Vegetation-form and ecological characters not studied, but being in so aberrant a position for a fern, it offers an inviting opportunity for the study of a proper physiological life-history.

POTENTILLA PALUSTRIS Scop. *Comarum palustre* L.—Also abundant and characteristic, but not studied ecologically.

With these occur several secondary forms, inclining usually to gregarious patches: *Eleocharis palustris* R. Br.; *Equisetum limosum* L. (*E. fluviatile* L.); *Eriophorum vaginatum* L., and other sedges; *Epilobium palustre* L.; *Phragmites communis* Trin. [*P. Phragmites* (L.) Karst.], locally called "quills"; *Vaccinium oxycoccus* L. [*Oxycoccus Oxycoccus* (L.) MacM.], and others, together with visitors from neighboring associations.

Characteristic of this region also, and also occurring to some extent on

[43] Omitted from *figs. 7, 8*, because when those were drawn I had intended to include this association in part with Macrospartinetum and in part with Caricetum, but further study of the subject makes it seem best to treat it as a distinct association.

[44] Identified for me by Dr. C. Warnstorf, of Neuruppin, Germany, the leading authority in this group.

the Macrospartinetum, are certain shrubs, *Myrica Gale* and *Salix discolor*, of which the former persists upon the floating bog.

To this as to the following associations I have given but little study, and have little of value to offer upon them. It is an aggressive association, constantly tending to move up upon the broadleaf marsh, the transition to which is of the most gradual character. Of all the associations of the marshland, this has the least definite boundaries, and indeed there is some question as to whether it deserves distinct rank.

IV. BOG FORMATION.

Consists of plants capable of existence in stagnant but pure water, showing, unless immersed, marked xerophytic characters (including reduction in size both of entire plant and of its parts) in adaptation to the lessened power of water-absorption by roots exposed to low temperatures.

The bogs occupy the entire marsh country above the heads of the tide on the rivers, and also places between rivers where drainage is obstructed, but their area has been much reduced in the marsh country by artificial processes of conversion back to marsh (*fig. 2* and p. 179). It includes three associations.

8. THE CAREX-MENYANTHES, OR FLOATING-BOG ASSOCIATION, OR CARICETUM.

By far the most extensive and characteristic bog association of the marshland, occupying the old marsh surface from near the head of tide on the marsh rivers to near the neighboring uplands (*figs. 2, 7*). The transition from the Aspidetum to the typical Caricetum is perfectly gradual, so that it is difficult to place a limit between the two associations. The marsh, as earlier fully explained (p. 173 and *fig. 4*), falls away gradually from tide-head, so that leaving behind the high marsh with its Phleumetum we reach a somewhat wet marsh with its Macrospartinetum and a constantly wet marsh with its Aspidetum, and finally come to a marsh with constant standing water above the surface, and here begins the Caricetum. The characteristic dominant plants are sedges of several species whose copious interlacing air-storing rootstocks form a mat, which floats upon the surface of the water as it deepens (*fig. 4*), and which becomes three or four feet in

thickness. It floats upon a foot or two of water, beneath which is the true marsh mud, blue for a few inches from the surface, and below that red to the bottom. As a rule the bog is firm enough to walk upon, though it trembles beneath the tread, but in places it is unsafe.

The dominant plants are, of course, the sedges, chief of which are the following:

Carex filiformis L., and *Eriophorum vaginatum* L., from the preceding association, are equally or nearly as characteristic of this; also *Carex stricta decora* Bailey, *Carex Magellanica* Lam., *Eriophorum gracile* Koch, and others.

With these are associated as a principal though hardly as a dominant member *Menyanthes trifoliata* L., the Buck-bean, which is especially abundant on the margins of streams and ponds, and with it is *Calla palustris* L. Among the sedges occurs some Sphagnum, but this, in the floating bogs, is by no means a dominant plant.

Upon this floating mat grow many other plants, many of them distributed in groups the determinants of which are not plain. Thus, especially near the transition occur large areas of very abundant *Equisetum limosum* L.; in other places *Eleocharis palustris* R.Br., is densely abundant. Further out large areas are nearly covered with *Typha latifolia* L. (cattails); again groups of *Phragmites communis* Trin. (quills) occur. *Myrica gale* L. is also abundant. Among less abundant plants are *Juncus Canadensis* J. Gay, and *J. Balticus litoralis* Engelm., *Sparganium simplex* Huds., *Sarracenia purpurea* L., *Drosera rotundifolia* L., *Epilobium linearis* Walt., and a few others. But I have not attempted to make a proper ecological study of these bogs, which I hope upon another occasion to consider much more fully.

9. THE HEATH, OR FLAT (SOLID) BOG ASSOCIATION, OR ERICETUM.

I have not attempted to make any ecological study of this association. It occurs mostly around the margin of the Caricetum on the parts furthest from the sea, and between the rivers, as at Sunken Island (*fig. 7*), and is readily distinguished by the presence of abundant trees of larch and black spruce, and

the abundant heath bushes.[45] In places on the floating bog, especially near its margin, one sees occasionally dense mats of Hypnum several feet across, indicating no doubt the beginning of flat bog formation. In general this association occurs at the oldest part of the bogs and hence probably represents the conditions towards which the floating bog is tending. It tends to occur also in strips along the contact of mainland and the Macrospartinetum, where it begins to merge into swamp, as later to be noticed.

10. THE SPHAGNUM, OR RAISED BOG ASSOCIATION, OR SPHAGNETUM.

In a few places only, near the margin of the Caricetum, occur small areas approximating to the true raised type of bog, consisting almost entirely of Sphagnum rising above the general water level of the basin, with dwarfed heath bushes but no trees, and generally showing the characters of *Hochmoor* which I have already described in the first work of this series. Small areas of this character also occur in the Sunken Island. But I have not tried to work out their relations to other types of bog, and the subject remains for future study.

V. WATER MARGIN FORMATION (NEMATIUM).

The marsh and bog rivers above the influence of the tide everywhere exhibit a dense marginal vegetation (Typha, Sparganium, Acorus, Lysimachia, Chelone, Dulichium, etc.) differing in different parts of marsh or bog, and divisible into three or four associations. I have not, however, made any attempt to study these in detail. Another association exists on the margins of the lakes, and yet another in the bottoms of the aboideaued streams. There is also of course a plankton formation in these streams, but I have not studied it.

VI. THE SWAMP FORMATION (HELORGADIUM).

In most places, at the contact of reclaimed marsh and upland, occurs a region of poor drainage in the form of a narrow strip. On the wet marsh, along with the Macrospartinetum, this strip is

[45] Not all trees on the bog, however, indicate the flat bog, for many of them, as shown by soundings made by engineers of the Misseguash Marsh Co., are growing upon islands slightly submerged by the bog.

usually occupied by flat bog (Ericetum), but on the dry marsh it is more likely to form a strip of swamp, with alders, black spruce, and blue flag. This forms at least one association, probably more, but I have not attempted to study it, and it remains for future investigation.

The succession of the plants of the marshland in space and in time.

The succession of the plants of the marshland within associations, both in space and in time, and of the associations within the formations, have been described in the preceding pages, but we may here summarize the subject and attempt to represent it graphically. Then we must consider the natural succession which takes place in the reclamation of the marshes.

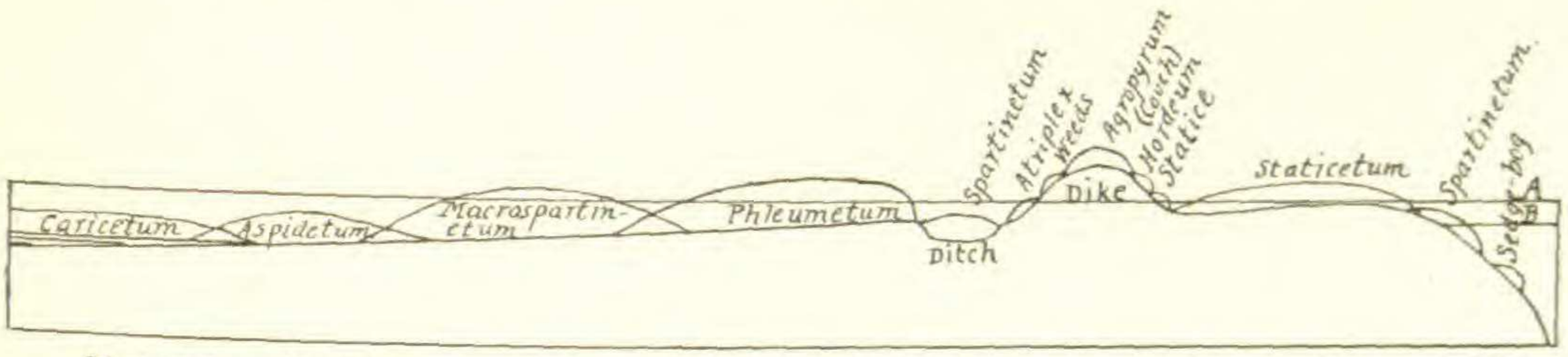

FIG. 15.—Diagram to show the distribution of the principal associations of the marsh land in relation to one another. The tops of the curves show the places of maximum development of the association, and the places where they overlap are the places of competition. *A* is extreme high tide level, and *B* ordinary high tide. The "ditch" is not a drainage ditch but one of those from which mud has been taken for the dikes.

The succession of the associations on the marshland is about as represented in *fig. 15*. The form given to each association is intended to represent its culmination at its optimum of size and vigor, and to show that the associations only mingle on their margins when their optima are past. These relations may be brought out in another manner and correlated with the distribution of the prepotent physical factors of water and salt, by means of the curves of *fig. 16*, which, however, it is to be remembered, are not constructed from actual measurements, but only ideally from observation. They have their chief interest as a prediction of the way in which such facts will ultimately be represented.

The distribution of the associations on the dikes is notable,

and needs some comments (*fig. 15*). The physical conditions upon the dikes are plain. The situation is a particularly well-drained one, but on the outer face of those exposed to the sea there must be more salt than upon the inner faces, due to the occasional wash of the sea at high tides during storms. At all events especially on the more exposed dikes, the outer slopes usually show a more halophytic facies than the inner. On both faces there is a distinct zonation, which differs somewhat in different places, but appears most characteristically, especially on dikes exposed directly to the sea or lower courses of the tidal rivers,

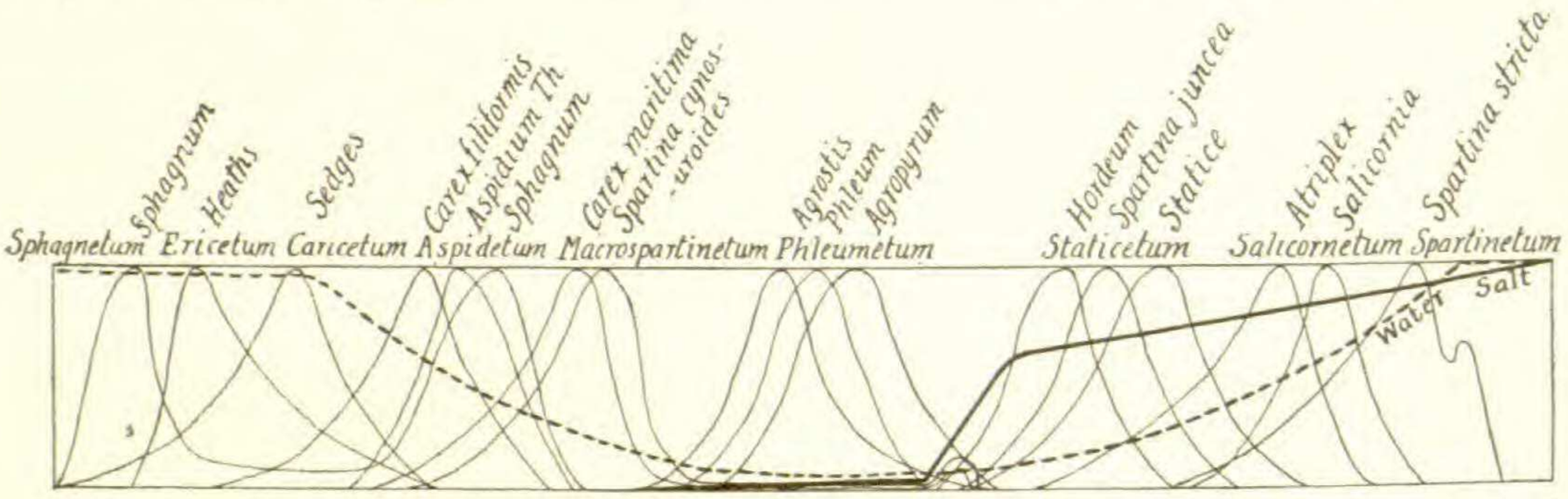

FIG. 16.—Diagram to show the distribution of the principal associations and of their prominent species in relation to the amounts of water and salt. The species curves show the approximate range of the forms within one another's habitat. The two members of the Macrospartinetum can endure some salt; hence their extension as here represented. The second summit of the Spartinetum represents the "sedge-bog."

to be as follows: On the outer face, the lowest zone, occupying the angle, is usually the Statice, but is sometimes Puccinellia; above this is a zone of Hordeum and above this the couch, the almost invariable dike grass, here evidently fully at home. Occasionally Atriplex occurs between Hordeum and couch. Now the Statice is the usual marginal member of the Staticetum, while the Hordeum comes in early upon that formation when maturing and the couch comes upon it later. There is plainly then upon the outer face of the dikes a general repetition of the order in the association, though the *Spartina juncea* is not, as far as I have noticed, in its place between Statice and Hordeum. The zonal arrangement, however, often shows Atriplex in place of the Statice, and the Hordeum may be wanting. On the inner face of the dikes, there is usually a band of Atriplex at the lower angle, especially when, as is usually the case, there is a row of

ditches containing stagnant and hence saltish water, just within the dikes, occupied by *Spartina stricta*. Above this Atriplex comes often, if not usually, a band of common roadside weeds, a part of the Cnicetum, while above it is the band and cap of almost invariable couch. This arrangement is sometimes different, and I have even seen a case where the top of the dike was occupied entirely by Atriplex, with a band of couch on each face of the dike below it, and other variants occur, the whole being much influenced by the position and age of the dike.

We pass now to consider another important phase of this subject, namely the natural succession of the plants on new marsh which is being reclaimed from the sea. It is rarely nowadays that a new piece of marsh is diked and reclaimed from the beginning, but what is practically the same thing occurs in numerous places, where the marsh is being renewed by the tide. When a piece or body of marsh shows a lessening of fertility, either through the growth of bog or other causes, the dikes are broken down and the tide admitted. The higher tides usually flow readily over it (an evidence, as I believe, of the gradual subsidence of the region), kill most or all of the vegetation upon it, and begin to deposit new mud. This is allowed to continue until several inches of mud have been laid down, a process requiring usually two or three years; then the dikes are re-built, the drains are opened, and the marsh is left to itself. A vegetation at once springs up upon it, which goes through a series of changes, ending in the development in four or five years of the Phleumetum or best timothy grass, and without any aid from man beyond keeping the drains in order. This succession can be followed in various places and is about as follows: When the tide first flows upon the marsh ,the plants show very diverse degrees of resistance to it. The bog plants, the various woody bushes, the clovers and the timothy are killed at once, it is said by a single tide. They turn white or brown and dry up, the bushes turning almost black, as if scorched by fire. On the other hand the watergrass, the broadleaf, the browntop, show a considerable degree of resistance, while the couch can stand

for some time on the higher tussocks.[46] I have not determined the exact cause of the death of these forms, but presumably it is due to the plasmolysis of the root hairs, and consequent loss of ability to absorb water, followed by a drying up. To this, of course, may be added some positively poisonous action of salt upon the protoplasm. The tide deposits layers of the rich mud, and upon this, while undiked, there tends to spring up a large development of the Salicornetum. In particular, there appears during the process of tiding an open growth of Suaeda, Salicornia, and Atriplex, all of which grow large and luxuriant. Of these the Suaeda appears to become most abundant, and is a large, diffuse, straggling plant quite superior to its small form on the river banks. The Salicornia also grows very luxuriantly, spreading diffusely in this situation. With these plants comes in some sedge, though I have not noticed that it becomes very abundant or luxuriant. Such appears to be the natural condition of marsh in reclamation. When the dikes are restored the first phenomenon observable is the large increase in size and abundance of these forms. They fill up the ground, and the Atriplex in particular grows even waist high. The remarkable luxuriance of the members of the Salicornetum under these conditions shows how far they are, upon the marshes, from occupying their optimum situation, from which they must be kept by the dominance of the other associations, a subject of much importance in connection with the nature of competition. But along with the increase in size, other forms immediately begin to come in, especially some members of the Staticetum, the *Spartina juncea*, Triglochin, and especially the Puccinellia, and the Hordeum, which is ubiquitous in such positions. Closely after these, however, comes the couch, and right after it the Agrostis. Such is the condition at the end of the first year, after which the timothy follows; and in the fourth year it becomes abundant. As the new forms come in the older tend to die out, so that finally, after a succession of forms answering to the natural succession in space on the marsh, the timothy takes natural

[46] This resistance is taken advantage of by some farmers, who admit the tide sparingly and are able to obtain some renewal without totally losing an annual crop. But it is not considered a profitable method.

possession, all the others except the couch disappearing. This, however, is the summit of the series; nowhere, excepting on the ridges along the ditches and in a few exhausted spots, where a low shrub vegetation appears, is anything higher developed. The timothy stands out as the best adapted plant in all this country to the conditions prevailing on the reclaimed marsh. In this process of reclamation, there is a grand opportunity to study the nature of competition, the problems of which, however, cannot be settled by observation alone, but must be attacked by experiment.

The above appears to be the normal succession upon places where high marsh is built; in the low places the succession is somewhat different, leading through watergrass ultimately to broadleaf, which by improvement in drainage may lead to couch and timothy. It is said by the farmers that the succession of plants depends much upon the way the drainage is managed.

There is another place in which the succession may be followed, namely in the lakes in process of reclamation, and I have seen it particularly well illustrated in Germantown Lake in Albert county, to which the tide is admitted by a canal. The tide has built into the lake long low points of marsh mud, which are at once taken possession of by a rank growth of *Spartina stricta* (sedge) immediately above which, on the higher parts, comes a dense growth of broadleaf. Right after the latter come scattered tufts of dense browntop, which is fairly abundant, and after this comes the couch. Here too is afforded a very favorable opportunity to study competition, which, however, I had not the time or means to utilize.

Conclusion.

The observant reader will not need to be told that the present study is highly defective and inconclusive, to a degree which no one can realize more than does its author. Yet this very defectiveness emphasizes an important lesson, for, while it is in part the fault of the author, it is not wholly so, but is in a large measure made necessary by the present imperfect state of our

ecological knowledge and methods. The study does make fairly clear, however, the directions in which research must now proceed, and upon this I desire to offer some comments.

The idea of ecological plant geography, the broadest and most important phase of ecology, is to interpret the physiognomy of vegetation; to tell precisely why each plant is where it is, in the company it is, and of the form, size, color, texture, etc. it is. Each plant, as it stands in nature, is an adjustment or equilibrium between its physiological powers and properties on the one hand, and the properties of the environment, physical and biological, on the other. Now, for a full understanding of these matters four principal things are needful.

First, a collection and description of the actual facts as to the kinds of plants which occur in a given region, as to their visible features, and as to the way in which they are grouped. Our present-day ecology, especially that which is being actively pursued in this country, is strong in this descriptive work, to which indeed it is well-nigh confined, and it is giving an excellent basis for future advance. In the present paper I think these facts about the marshland vegetation are fairly represented. Even from this point of view the study is defective in one respect, common to most of our ecological studies, namely, the descriptions apply to the summer only; if followed through the year (as it should, but for practical reasons could not, be), it might, and probably would, lead to conclusions somewhat different in details, as well as to much additional knowledge.

Second, an exact study and clear expression of the facts as to the physical features of the environment which can affect plant life. For the study of the physics of the atmosphere, the methods have been thoroughly organized by meteorologists, but we need some way of expressing meteorological results in a form for ecological use. It is very common in ecological papers, as in the present one, to give elaborate tables of temperature, precipitation, etc., and then to dismiss them with a few words of general comment. This shows either that meteorological data are obtainable more copiously and exactly than needful for ecological use, or else, as is more likely, they are not expressed in a

form in which we can make ecological use of them. Some advance has been made in this direction by such curves as Drude uses in his *Hercynische Florenbezirk* (p. 71), but these need further development. In the study of the physics of the soil, however, the ecological importance of which is becoming constantly more manifest, it is very obvious that, despite the rapid advances now being made, the methods of investigating and of representing the facts are still far from developed and wholly insufficient for ecological uses. The extension of knowledge in this direction is, I believe, the greatest desideratum of ecology for the near future. In thus emphasizing the deficiencies of our knowledge of the physics of the plant's environment from the ecological point of view, I would not underrate the positive knowledge we have, which is considerable. But it is notable that this knowledge is of a very general sort and not expressible in definite ecological form, as shown by the general and even hazy way in which it is commonly stated in current ecological literature, including the present paper. In fact, vague generalization and nimble guessing (much of it, no doubt, good guessing, but still guessing) are more characteristic of the physical part of our current ecological literature than is precise statement; and the expressions "probably," "doubtless," "in a general way," form a considerable part of present ecological language. All this is evidence that in our ecological discussions we have reached about the limit of possible advance with our present knowledge of the physics of the environment and of how to use the knowledge we have. Indeed, this point was reached some time ago, and much of recent ecological literature has been so barren of real advance as to bring upon ecology a reproach which it must be admitted it largely deserves. This is the more unfortunate since even the methods of ecological description have not substantially improved. I can say this with the greater frankness since my own study herewith presented so obviously reflects the prevailing formalism and deficiencies in this respect, though I have made some attempt to improve at least the method of description of the vegetation. There can be no question, I believe, that further substantial eco-

logical advance is not possible until we make a direct attack from the ecological standpoint upon the subject of the investigation and representation of the facts of the environment, especially of the soil. Now this obviously cannot be done, as most ecological work is now being done, by busy teachers who can devote to field work only a few weeks of their summer vacations. It can only be accomplished by the systematic work of trained investigators, who, with a fully and properly equipped laboratory established in the field at the place to be investigated, and with ample assistance to aid in the mechanical work, can devote their entire time to the subject for months or years until the problems are solved for that region. The laboratory must obviously be in the field, since the conditions vary so much in the different seasons and under the various local conditions. Thus, and thus only, I believe, can we make any further real advance in ecological plant-geography.

Third, there must be made a thorough study not only of the structure and development of the important plants which give character to the different parts of a vegetation, but also of their physiological characteristics quantitatively expressed. Thus, we need to know for each kind of dominant plant its transpiration power, and the extent of its possible regulation under various circumstances; its water-absorbing power; its capacity for air storage; its power and limits of resistance to salt or other unfavorable substances and influences; its cardinal temperature-points for growth and for its other physiological properties. For this study it is indispensable that methods and apparatus be developed by which the various facts may be ascertained with ease and precision, and the results expressed or represented in a form to make them available for ecological use, that is, so that they may be compared and correlated with the physical data. Very important in this connection is the determination of the physiological plasticity of the plant, and in how far adaptation to a new influence weakens or destroys adaptation to an older. Hitherto, in our studies of adaptation we have laid great stress upon the study of structures in relation to adaptation to environment, and much knowledge of this subject has been accumu-

lated, while physiological adaptation, the study of the accommodation of the protoplasm itself to outside influences, has received little attention. Yet this is the most important subject of all in adaptation; for structure, so far from representing the important feature in the adaptation of the plant to its environment, is simply an external manifestation of the way in which the protoplasm brings itself into better touch with the environment. It is an expression of a degree of physiological properties, and it is the properties and powers of the protoplasm itself which is the important thing. All such data are essential to the full understanding of the real nature of the vegetation-forms, those units of the ecologist; and in this direction, viz., the determination of physiological life histories of important plants, there lies not only an indispensable approach to future advance in ecology, but a most attractive field of research for its own sake. Such studies, and such only, will enable us to understand the true natural history of individual plants, and will help to bring the day when our "manuals," in addition to giving us the details upon which the classification of our plants is based, will give us also such information about their lives and habits as will enable us to understand their places in nature. These studies may in part be followed in university laboratories, but for the most part they can be carried on only in field laboratories, such as have already been mentioned as needful for the study of physical problems, and here both classes of problems, similar in general methods and inseparable in results, can best be investigated together.

Fourth, a knowledge of the true nature of plant competition and cooperation is essential. The fullest knowledge of the physical environment, and of the power of the plant to respond to it, would only enable us to explain the general situation and vegetation-form of plants in cases where each individual was free from any interference from others. But in fact, as we know, plants are rarely or never so situated, for, massing together, they profoundly affect one another's distribution and form. The study of vegetation, therefore, of masses of plants, involves this important element of their effects upon one

another. Or we may express the situation thus. Ecological plant geography is the study of the actual adaptations of masses of plants as they grow together in nature. The physics of the environment, plus the physiological properties of the plant, tend to give as a resultant a certain general vegetation-form; this, plus cooperation and competition, gives the actual groupings in a vegetation.

That plants do in some way compete with one another, that upon the same ground some kinds can drive others out and take possession, is, of course, evident to observation. That, on the other hand, certain kinds of plants can combine and cooperate for the common good is, I think, equally true. In both cases we know some of the general causes which determine the results of both competition and cooperation, but as to the details we know nothing. Seven years ago Warming, in his great book, said: "There is scarcely a more attractive biological field than to determine what the weapons are with which plants force one another from their positions," but today we know no more of that subject than when Warming wrote those words. Yet ecological plant geography cannot advance, nor can we understand the vegetation of a country or district, until we understand this subject, and we but blind ourselves and only imperfectly convince others by our present generalizations. The crucial point in competition is this: by what weapons or methods does one plant overcome another, when the result is determined between the plants and not by the environment. In a broad way we can often see general reasons why one plant should dominate another; the more rapid growth of one kind, or larger size, or the replacement of a shade-loving by a sun-loving kind, or the entrance of a new kind when one form has exhausted the needed minerals from a soil, etc., seem to give an ample explanation. But even in these cases, and especially in the many cases where the kinds seem evenly matched, we do not know precisely the method by which one kind manages to displace another. It is obviously by means of no visible carnal weapons such as animals use, nor is it a mechanical forcing aside of a weaker kind, for often there is ample standing room for the vanquished with the victor.

Some of the phenomena of competition seem to imply that each plant is able to control by some chemical or other method still unknown, a certain sphere of influence about it, a limited area of space of which it is the center and from which it can exclude others, and that this sphere of influence, like other adaptive features of the plant, is modifiable adaptively. Gregarious forms would be such as grow together so closely that these spheres touch, excluding other forms, and before the advance of such a phalanx other forms of lesser vigor must all go down. Elsewhere these spheres, rigidly maintained against an enemy, might be relaxed to admit a friendly or cooperating form, and other of the phenomena commented upon in the preceding pages, might find an illuminating explanation in such a conception. But it is all pure speculation, and can be settled only by careful field experiment. Until this is given we shall not know whether associations are mere mixtures, or are to some extent cooperative communities, and if the latter, what the nature is of the bonds which unite their members. I have no question that in a properly equipped field laboratory, such as has already been mentioned, competent investigators, working with an experimental piece of ground, could solve this most vital of questions. Fortunate will he be who first has the proper opportunity to attack it!

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